

New Hosts of Western Cherry Fruit Fly, *Rhagoletis indifferens* (Diptera: Tephritidae), and Their Relationship to Life History Characteristics of This Fly

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ABSTRACT Two native trees and one introduced tree in the coast forest ecosystem in southwestern Washington state were identified as new host records for the western cherry fruit fly, *Rhagoletis indifferens* Curran (Diptera: Tephritidae), in 2002 and 2003. Key life history characteristics of flies on or from the new hosts also were examined. Rearing of larvae to adults confirmed native cascara, *Rhamnus purshiana* DC.; black hawthorn, *Crataegus douglasii* Lindl.; and introduced cherry laurel, *Prunus laurocerasus* L., are suitable developmental hosts. In addition, two flies reared from cascara had wing patterns apparently not reported previously, with one keying out to *R. indifferens*. The numbers of larvae that emerged from fruit of the new hosts and a known host, bitter cherry, *Prunus emarginata* (Dougl. ex. Hook) D. Dietr., were lower than from fruit of sweet and sour cherries, *Prunus avium* (L.) L. and *Prunus cerasus* L. Seasonal patterns of adult abundance in cascara, black hawthorn, and cherry laurel as determined by catches on unbaited sticky yellow panel traps were similar to those in bitter cherry, with most flies caught beginning in mid-July after fruit were no longer green. Fruit of all hosts ripened at similar times. On cascara and black hawthorn, *R. indifferens* was observed feeding on damaged fruit, and on black hawthorn, flies mated with the non-native apple maggot, *Rhagoletis pomonella* (Walsh). The longevity of flies reared from cascara, bitter cherry, and sweet and sour cherry was similar, averaging 55.5–83.4 d, and was higher than that of flies reared from cherry laurel, which averaged ≤ 46.2 d. Body mass of flies from cascara, cherry laurel, and bitter cherry was lower than that of flies from sweet cherry. In contrast to the coast forest ecosystem, neither cascara nor cherry laurel was found at sites studied in ponderosa pine and sagebrush–bunchgrass ecosystems in central Washington in 2003 and 2004. Adults were not caught on unbaited traps in black hawthorns in these two ecosystems, and no larvae were reared from hawthorn fruit from either ecosystem.

KEY WORDS *Rhagoletis indifferens*, cascara, black hawthorn, cherry laurel, bitter cherry

HOST USE BY THE western cherry fruit fly, *Rhagoletis indifferens* Curran (Diptera: Tephritidae), the major insect pest of introduced sweet and sour cherries, *Prunus avium* (L.) L. and *Prunus cerasus* L., respectively, in the northwestern United States (Bush 1966), has been well documented in or near commercial cherry-growing areas. To date, *R. indifferens* has been reported to infest only *Prunus* spp. (Rosaceae). The fly was first recorded on introduced cherries in 1913 (Frick et al. 1954, Bush 1966) and on native bitter cherry, *Prunus emarginata* (Dougl. ex. Hook) D. Dietr. in 1931 (Curran 1932). Introduced Mahaleb cherry, *Prunus mahaleb* L. (Little 1995) was referred to as a “variety” that was susceptible in 1954 (Frick et al. 1954). Hosts that apparently are rarely used are native choke cherry, *Prunus virginiana* L. variety *demissa* (Nutt.) Torr. (Simkover 1953, Frick 1957, Madsen 1970, Banham 1971); introduced Japanese plum, *Prunus salicina* Lindl.; and introduced Pacific plum, *Prunus subcordata* Benth. (Ellertson 1961). Although the major hosts in or near commercial cherry-growing

areas in the fly’s non-native sagebrush–bunchgrass ecosystem are known, little is known about host use in the fly’s native coast forest ecosystem. The high tree diversity and abundance in this ecosystem make the potential use of other hosts greater here than in the interior ponderosa pine and sagebrush–bunchgrass ecosystems.

Identification of new hosts and ecological and behavioral information about *R. indifferens* in relation to the new hosts are of interest, because they may shed light on the evolution of host finding and acceptance in tephritids. With respect to host use, tephritids have been classified as monophagous (use of one host), stenophagous (use of plants in a single genus), oligophagous (use of plants in a single family), or polyphagous (use of plants in several families) (White et al. 2000), but why species vary so much in the numbers of hosts used is not well known. One proposal is that monophagous or stenophagous species tend to be chemical, visual, and tactile specialists with respect to host cues used to find and accept oviposition sites,

whereas polyphagous species, which have received the most attention, tend to be chemical, visual, and tactile generalists (Díaz-Fleischer et al. 2000). In the apple maggot, *Rhagoletis pomonella* (Walsh), host use is broad, with ≈ 33 species of non-native and native hosts recorded, all in the Rosaceae (Smith and Bush 2000). Although not typical, this indicates *Rhagoletis* species have the ability to use numerous plants for larval development. Indeed, trapping studies in 2001, 2002, and 2003 in the coast forest ecosystem in Washington state suggested that *R. indifferens* may use at least three previously unrecorded trees that are taxonomically very different from one another as hosts: native cascara, *Rhamnus purshiana* DC.; native black hawthorn, *Crataegus douglasii* Lindl.; and introduced cherry laurel, *Prunus laurocerasus* L. Cascara is a wide-ranging, relatively uncommon tree found in low foothills in damp, shady places in Washington mostly near the coast, whereas black hawthorn is a wide-ranging, common tree found in Washington from low- to middle-mountain elevations, mostly in coast forest and ponderosa pine ecosystems (Lyons and Merilees 1995). Cherry laurel is an evergreen native to central and western Asia (Islam 2002) that is abundant in Washington west of the Cascades (Hitchcock and Cronquist 1973). Flies also were observed feeding on juice of cascara fruit, stinging cascara fruit, and mating on two cascara trees in 2002 (W.L.Y., unpublished observations). Despite these behavioral observations and trap catches of flies on the trees, confirmation that cascara and the other trees are suitable for larval development is lacking. Whether *R. indifferens* is a chemical, visual, and tactile specialist or generalist might be inferred from the use of these plants. New discovery of hosts also may provide clues to future host range expansion and in host race formation in *Rhagoletis*, topics that have garnered much interest (Bush 1969a, Diehl and Bush 1984, Feder et al. 1995).

The current study was undertaken to determine whether these and other plants are used as hosts by *R. indifferens* and to determine life history characteristics of flies reared on these new hosts. Specific objectives were to determine the relationships between new hosts and larval infestation levels, seasonal adult abundance, adult activities, fly longevity, size, and use of hosts in different ecosystems. These relationships and possible host race formation in *R. indifferens* are discussed.

Materials and Methods

Field Sites in the Coast Forest Ecosystem. Studies in the coast forest ecosystem were conducted in 2002, 2003, and 2004 at 39 sites (defined here as locations ≥ 1.6 km apart) scattered within 40 km north, northeast, and east of Vancouver (45° 37.45' N, 122° 39.78' W) in southwestern Washington state, encompassing an area of $\approx 1,250$ km². A sampled site occupied ≈ 30 m² (single tree) to ≈ 1.5 km² (if >100 trees). Elevations of sampled sites were 3–305 m (mean \pm SE, 104 \pm 14 m). Almost all trees were feral and occurred in rural, natural habitats, and less fre-

quently, homeowners' yards. Annual rainfall in the Vancouver area is 990 mm, and mean monthly temperatures are 3–18°C (Hoare 2003).

Identification of Emerged Flies and Larval Infestations of Fruit. In 2002 and 2003, fruit were sampled from cascara; black hawthorn; cherry laurel; bitter cherry; sweet and sour cherries; Asian pear, *Pyrus serotina* L.; common pear, *Pyrus communis* L.; garden plum, *Prunus domestica* L.; cotoneaster, *Cotoneaster* spp.; apple, *Malus domestica* Borkh.; ornamental hawthorn, *Crataegus monogyna* Jacq.; crabapple, *Malus* sp.; rose, *Rosa* spp.; quince, *Cydonia oblonga* P. Mill.; and mountain ash, *Sorbus* sp. Each tree species was sampled from one to 13 of the 39 sites at least once from July to October, depending on species abundance, fruit loads, and the trees' accessibility. Within a given site, one to 12 trees of one species were sampled (Table 1). Not every site had all tree species, and most had only one or two species. Collection dates varied among plant species, reflecting differences in fruiting phenology. In 2004, due to labor constraints, emphasis was placed on collecting cherry laurel and sweet and sour cherries (Table 1). We held fruit in tubs at ≈ 10 –21°C and counted larvae that emerged after 8 wk or until fruit dried. In 2002–2004, pupae were stored at 3–4°C in moist soil for ≥ 6 mo. After this period, they were transferred to 20–27°C and 30–40% RH for adult emergence and later identified using keys in Foote et al. (1993). Voucher specimens were deposited in the Essig Museum of Entomology at the University of California, Berkeley, CA.

Seasonal Adult Fly Abundance. Cascara and black hawthorn were strongly suspected as hosts based on preliminary trap catches in 2001. In 2002 and 2003, seasonal adult abundance patterns on these trees and a known host were compared. Unbaited 14 by 23-cm sticky yellow panel traps (Scenturion, Clinton, WA) were hung in cascara, black hawthorn, and bitter cherry. Traps were not baited, because the objectives were to determine fly presence within trees and to reduce chances of drawing flies in from surrounding trees. One or two traps were hung 1.5–2 m above ground in each of four to 26 trees of each species. Some of the trees were the same ones used to determine larval infestations of fruit. Traps were deployed from 23 May to 5 July and were checked once or twice a week until 20 August to 15 September. Cherry laurel was strongly suspected as a host based on preliminary trap catches in late 2003. Thus, in 2004, one or two unbaited sticky yellow panel traps also were hung in each of five cherry laurels at five sites in rural areas and homeowners' yards from 15 May to 15 September. Traps were checked every 3 to 15 d. Fruit colors based on visual examinations were recorded periodically. In all studies, flies were removed from traps using forceps and stored in 70% ethanol. Flies were cleaned of adhesive with citrus solvent (Orange-Sol Household Products, Gilbert, AZ) and identified.

Adult Fly Activities on Trees. In 2003, to determine the use of suspected host plants by adult flies, observations of fly activities on black hawthorn and cascara trees were made at one site along the Columbia River

Table 1. Trees sampled, sampling periods, numbers of sites (locations ≥ 1.6 km apart) sampled, and numbers of fruit collected in sites in the coast forest ecosystem of southwestern WA, 2002–2004

Tree species	Sample period	No. sites	No. trees	Samples/tree	Fruit/tree/date
2002					
Cascara	31 July–18 Sept.	4	8	1–5	88–982
Black hawthorn	31 July–10 Sept.	1	6	1–2	88–478
Bitter cherry	1 Aug.–12 Sept.	13	13	1–3	40–2,225
Sweet/sour cherries	1 June–1 July	4	6	1	78–220
Asian pear	27 Aug.–10 Oct.	1	1	3	15–35
Common pear	21 Aug.–28 Sept.	4	10	1–2	12–101
Garden plum	21–28 Aug.	3	3	1	20–80
Crabapple	22 July	1	1	1	88
Rose	19 Sept.–4 Oct.	1	2	1	116–278
Quince	25 Oct.	1	1	1	13
2003					
Cascara	16 July–27 Aug.	9	20	1–5	25–500
Black hawthorn	23 July–11 Sept.	5	11	1–5	25–664
Cherry laurel	12 Aug.–21 Sept.	6	7	1–3	51–265
Bitter cherry	10 July–27 Aug.	13	16	1–3	25–541
Sweet/sour cherries	13 June–17 July	10	33	1–3	10–305
Asian pear	19 Aug.–10 Sept.	4	5	1–2	6–60
Common pear	4 Aug.–7 Oct.	7	16	1–2	6–49
Garden plum	20 Aug.–3 Sept.	6	6	1	7–217
Cotoneaster	30 Sept.–19 Oct.	6	8	1	123–938
Apple	26 July–18 Oct.	10	28	1	15–126
Ornamental hawthorn	25 Aug.–20 Oct.	9	19	1–2	137–1,014
Crabapple	26 July–20 Oct.	7	7	1	20–103
Rose	11 Aug.–17 Oct.	6	10	1	43–720
Quince	10 Sept.–15 Oct.	3	3	1	5–21
Mountain ash	5 Aug.–6 Oct.	5	5	1	95–119
2004					
Cherry laurel	5 Aug.–8 Sept.	5	5	1–3	198–750
Sweet/sour cherries	10 June–16 July	4	28	1–2	160–542

in Skamania County (45° 35.88 N, 122° 07.03 W; elevation 11 m) between 0800 and 1800 hours. Searches for flies on leaves and fruit of trees were made at all cardinal points up to 2.5 m above ground. Flies on three black hawthorns were observed for 40–135 min each (9.4 total h) on 7 d from 18 July to 5 August. Periodic observations of flies on three cascara trees also were made during trap inspections between 3 June and 15 September. Numbers of flies resting, feeding, mating, or engaged in other activities were recorded.

Fly Longevity, Size, and Fecundity. Longevity, size (mass), and fecundity of flies reared from new hosts and bitter cherry from the 2002 and 2003 fruit collections were compared. Flies from sweet cherry used for comparisons originated from fruit collected in central Washington in 2002 and 2003. Tests were conducted at 20–27°C, 30–40% RH, and under a photoperiod of 16:8 (L:D) h. For 2002 collections, a male and female from cascara, bitter cherry, or sweet cherry were paired whenever possible inside a 0.473-liter paper container and provided a dry 20% yeast–80% sugar diet on a 1.5-cm² paper strip and water on a cotton wick. However, due to different numbers of males and females that emerged, males and females were not always paired. Eight days after emergence, a sweet cherry ('Bing') was placed in the container. Individual cherries were removed every 3 d and replaced with new cherries until flies died. Deaths were recorded daily. Eggs were removed from fruit and counted. For 2003 collections, similar procedures were followed using flies from cascara, black hawthorn, cherry laurel,

bitter cherry, and sweet cherry, but no data on fecundity were gathered because fresh cherries were not available. For both collections, dead adults were dried in an oven at 145°C for 30 min and weighed on a microbalance (Sartorius, Goettingen, Germany). Numbers of flies tested were one to 27 per sex per host, depending on emergence. Host fruit mass was determined by weighing 10–15 mature fruit collected from each of two to 13 sites in 2003. Ten sweet cherries also were weighed.

Presence of and Use of New Hosts in Other Ecosystems. In 2003 and 2004, attempts were made to locate cascara, black hawthorn, and cherry laurel within ponderosa pine (≤ 10 km northwest and southeast of 46° 50.98' N, 120° 57.23' W; area studied ≈ 50 km²; elevations 610–640 m) and sagebrush–bunchgrass ecosystems (≤ 88 km northwest and southeast of 46° 25.13' N, 120° 16.02' W; area studied ≈ 400 km²; elevations 124–333 m) in central Washington. Annual rainfall and mean monthly temperatures in the ponderosa pine ecosystem sites are ≈ 250 mm (Lyons and Merilees 1995) and about –8 to 23°C, respectively, and in the sagebrush–bunchgrass ecosystem sites, 190–200 mm, and –6 to 30°C, respectively (Hoare 2003). Extensive searches in these ecosystems yielded only black hawthorn. Bitter cherry was found in the ponderosa pine ecosystem but not in the sagebrush–bunchgrass ecosystem, which had only sweet and sour cherry trees as known common hosts.

In 2003 in the ponderosa pine ecosystem, single unbaited sticky yellow panel traps were hung in 11 black hawthorns and also in 30 bitter cherry trees from

Table 2. Larval *R. indifferens* infestations of fruit at representative sites (locations ≥ 1.6 km apart) in the coast forest ecosystem of southwestern WA, 2002–2004

Tree species	% sites positive ^a	% trees positive ^a	Total fruit	Total pupae ^b	Larvae/fruit/tree/site \pm SE
2002					
Cascara	75.0	75.0	3,885	94	0.019 \pm 0.010a
Black hawthorn	0	0	2,095	0	— ^c
Bitter cherry	92.3	92.3	6,059	615	0.125 \pm 0.027a
Sweet/sour cherries	100.0	83.3	808	26	0.031 \pm 0.010a
2003					
Cascara	44.4	35.0	5,365	30	0.003 \pm 0.001a
Black hawthorn	20.0	16.7	5,194	3	—
Cherry laurel	66.7	71.4	1,772	154	0.051 \pm 0.029a
Bitter cherry	100.0	100.0	7,037	933	0.160 \pm 0.019a
Sweet/sour cherries	100.0	78.8	1,114	443	0.357 \pm 0.123b
2004					
Cherry laurel	60.0	60.0	2,702	40	0.013 \pm 0.007a
Sweet/sour cherries	100.0	71.4	7,894	799	0.195 \pm 0.087b

Larvae per fruit per tree per site or larvae per fruit per tree within years followed by same letter are not significantly different (ANOVA, Fisher's LSD test, $P > 0.05$).

^a Number of sites and trees shown in Table 1.

^b Only *R. indifferens* emerged in 2002–2004, except from black hawthorn (mostly *R. pomonella*) and bitter cherry (two *R. fausta*).

^c Emergence, larvae/fruit unknown because most pupae were *R. pomonella*.

7 July to 15 September to determine whether flies were visiting trees. Trees were located at three sites. Traps were checked twice per week. In addition, fruit (two to 300 per tree) were collected from these trees once a week from 28 July to 15 September to determine larval infestations. In 2003 in the sagebrush-bunchgrass ecosystem, fruit from eight black hawthorns (six to 874 per tree) were collected once between 9 June and 14 August. Fruit (130–1,111 per tree) from 27 sweet and sour cherry trees also were collected once during this period to establish fly presence and infestations in the area. Trees varied greatly in fruit loads, even when they were only ≈ 1.6 km apart, resulting in wide ranges in fruit sample sizes.

In 2004 in the ponderosa pine ecosystem, fruit from 40 black hawthorns (153–881 per tree) were collected once between 10 and 17 August. In the sagebrush-bunchgrass ecosystem, fruit from 22 black hawthorns (122–260 per tree) also were collected once during this same period. In both 2003 and 2004, fruit were held at 27°C for 4 wk for larval emergence. Pupae obtained from fruit were stored at 3–4°C in moist soil for ≥ 6 mo. After this period, they were transferred to 20–27°C and 30–40% RH for adult emergence.

Statistics. Larval infestation, longevity, fly mass, and fecundity (after square root ($y + 1$) transformation) data were analyzed with one-way analysis of variance (ANOVA). Fisher's least significant difference (LSD) test was used for mean separation (SAS Institute 2001).

Results

Identification of Emerged Flies and Larval Infestations of Fruit. Of the plant species sampled, only cascara, black hawthorn, and cherry laurel were confirmed as new developmental hosts of *R. indifferens*, although further sampling involving greater sample sizes and more plant species may reveal other fruit are hosts. Cascara fruit collected in 2002 and 2003 pro-

duced totals of 12 (eight males, four females) and eight (four males, four females) *R. indifferens*, respectively. Black hawthorn fruit collected in 2003 from two trees produced two female and one male adult *R. indifferens*. Cherry laurel fruit collected in 2003 and 2004 produced totals of 29 (11 males, 18 females) and nine (five males, four females) adult *R. indifferens*, respectively. Total numbers of fruit collected from the three hosts are shown in Table 2.

Two female flies reared from cascara had wing patterns apparently never reported before. One keyed out to *R. indifferens* (Foote et al. 1993), but the medial crossband on the wing was joined to the subapical crossband by a thin connection between the $M_1 + 2$ and $M_3 + Cu_1$ veins (terminology of Bush 1966), absent in typical *indifferens* (Fig. 1A and B) (male wing shown in Fig. 1A because wings of females were tattered after they were used in longevity tests below). In the other, not included as *indifferens*, the medial and subapical crossbands were joined by a thicker connection between $M_1 + 2$ and $M_3 + Cu_1$ veins (Fig. 1C). In addition, the apical crossband was not forked as in typical *indifferens* nor was there an apical spot. The lower edge of the apical crossband was located below the R_{4+5} vein but above the $M_1 + 2$ vein, which is the location of the edge of the upper fork prong in *indifferens* (Fig. 1A). The overall wing and body coloration was the same as in *indifferens*.

Larvae emerged from cascara, cherry laurel and black hawthorn fruit during 2002–2004 (Table 2). Larval infestations in cascara were lower than in bitter cherry, cherry laurel, and sweet and sour cherries, although the differences were not significant (Table 2). In 2002, infestation levels in cascara, bitter cherry, and sweet cherry were not different ($F = 3.32$, $df = 2, 18$; $P = 0.0594$), but in 2003, levels in cascara, cherry laurel, and bitter cherry were all lower than in sweet and sour cherries ($F = 5.32$; $df = 3, 34$; $P = 0.0041$). In 2004, the level in cherry laurel was also lower than in sweet and sour cherries ($F = 5.62$; $df =$

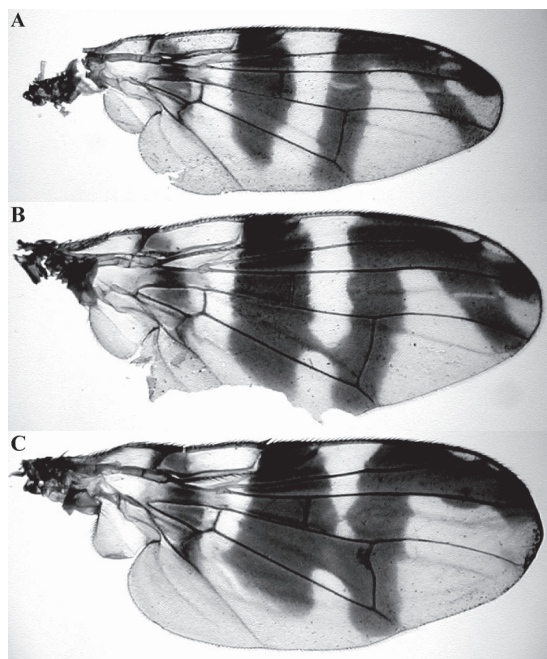


Fig. 1. Wing patterns of *Rhagoletis* flies reared from fruit of cascara, *Rhamnus purshiana* De Candolle, collected in southwestern Washington in 2003. (A) *R. indifferens*, male, typical pattern. (B) Fly keyed to *R. indifferens*, female. (C) Unidentified species, female. Wing lengths (rear of alula to tip): 2.69 mm (A), 3.04 mm (B), 2.96 mm (C); photos to the same scale.

1, 7; $P = 0.0496$) (Table 2). Most larvae from black hawthorn were *R. pomonella*.

Seasonal Adult Fly Abundance. In 2002 and 2003, *R. indifferens* were caught on unbaited traps in cascara and black hawthorn and in 2004 on cherry laurel (Fig. 2). Population trends on these three hosts and on bitter cherry in 2002 and 2003 were similar, with flies usually first caught in mid-July and fly numbers peaking in late July or August (Fig. 2). Few flies were caught when fruit were green. Numbers were highest when fruit were ripening or ripe (Fig. 2).

Adult Fly Activities on Trees. In 2003, *R. indifferens* were seen on all three black hawthorns on all 7 d of observations, with 67 total flies on fruit and 37 total flies on leaves. Two flies were feeding on damaged fruit, and nine were stinging fruit. Eight pairs were mating. Coupling on black hawthorn between *R. indifferens* and the non-native apple maggot, *R. pomonella*, also was seen on 3 d. On two of three cascara trees, seven flies were on leaves and five on fruit. One pair was mating, and one female was stinging fruit.

Fly Longevity, Size, and Fecundity. Longevity and mass of flies from different hosts differed, although fecundity among flies from cascara, bitter cherry, and sweet cherry did not differ (combined 2002 and 2003 data) (Table 3). Male *R. indifferens* reared from cascara and bitter cherry had similar longevity as those from sweet cherry, but those from cherry laurel had

shorter longevity than those from bitter cherry ($F = 3.53$; $df = 3, 69$; $P = 0.0192$). Males from cascara were smaller than those from cherry laurel, bitter cherry, and sweet cherry ($F = 4.77$; $df = 3, 67$; $P = 0.0045$). Females from cherry laurel had shorter longevity than those from bitter and sweet cherry ($F = 3.05$; $df = 3, 75$; $P = 0.0336$), and females from cascara, cherry laurel, and bitter cherry were smaller than those from sweet cherry ($F = 6.15$; $df = 3, 64$; $P = 0.0010$) (Table 3). Some females failed to lay any eggs, but zero values were included in the analysis. All four flies from cascara laid eggs; three of 27 flies from bitter cherry and one of 11 from sweet cherry failed to lay eggs. Sweet cherry was the largest fruit (mean \pm SE, $10,503 \pm 196$ mg). Cherry laurel ($2,181 \pm 232$ mg) was larger than cascara (444 ± 29 mg), bitter cherry (395 ± 61 mg), and black hawthorn (424 ± 34 mg).

Presence of and Use of New Hosts in Other Ecosystems. In 2003, traps in black hawthorn located in the ponderosa pine ecosystem did not catch any *R. indifferens*. However, most traps (97%) in bitter cherry caught *R. indifferens*. In 2003 and 2004, no *R. indifferens* larvae were reared from hawthorns from either the ponderosa pine or sagebrush-bunchgrass ecosystem, even though bitter and sweet and sour cherry fruit collections established flies were present in these areas. In 2003 in the ponderosa pine ecosystem, there were 0.102 ± 0.021 larvae per bitter cherry fruit per tree. In 2003 in the sagebrush-bunchgrass ecosystem, there were 0.604 ± 0.160 larvae per sweet and sour cherry fruit per tree. All flies that emerged from pupae from bitter and sweet and sour cherries were *R. indifferens*. These data showed flies were present and suggested that flies did not use black hawthorn in these ecosystems.

Discussion

In the coast forest ecosystem, larvae of *R. indifferens* infested fruit of cascara, black hawthorn, and cherry laurel, three previously unrecorded hosts, at relatively low levels. The infestation levels of the new hosts and of bitter cherry were lower than of sweet and sour cherries for several possible reasons. First, flies may prefer to oviposit in sweet cherries, because flies from central Washington laid more eggs in sweet than bitter cherries in laboratory choice tests (Simkover 1953). Second, the new hosts and bitter cherry may bear lighter or less consistent fruit loads than sweet and sour cherries, preventing large populations from building up on them. Third, the relatively low numbers of new hosts in relation to established sweet and sour cherry trees may provide fewer resources for activities such as oviposition, feeding, and mating. Fourth, parasitoids may have caused higher fly mortality in cascara, black hawthorn, and bitter cherries (all 7–9 mm in diameter), as they may reach larvae with their ovipositors more easily in the small fruit of bitter cherry (Frick et al. 1954) than in the larger fruit of sweet and sour cherries (16–28 mm in diameter).

Cascara was locally abundant and produced *R. indifferens* adults for 2 yr, suggesting it is not an inci-

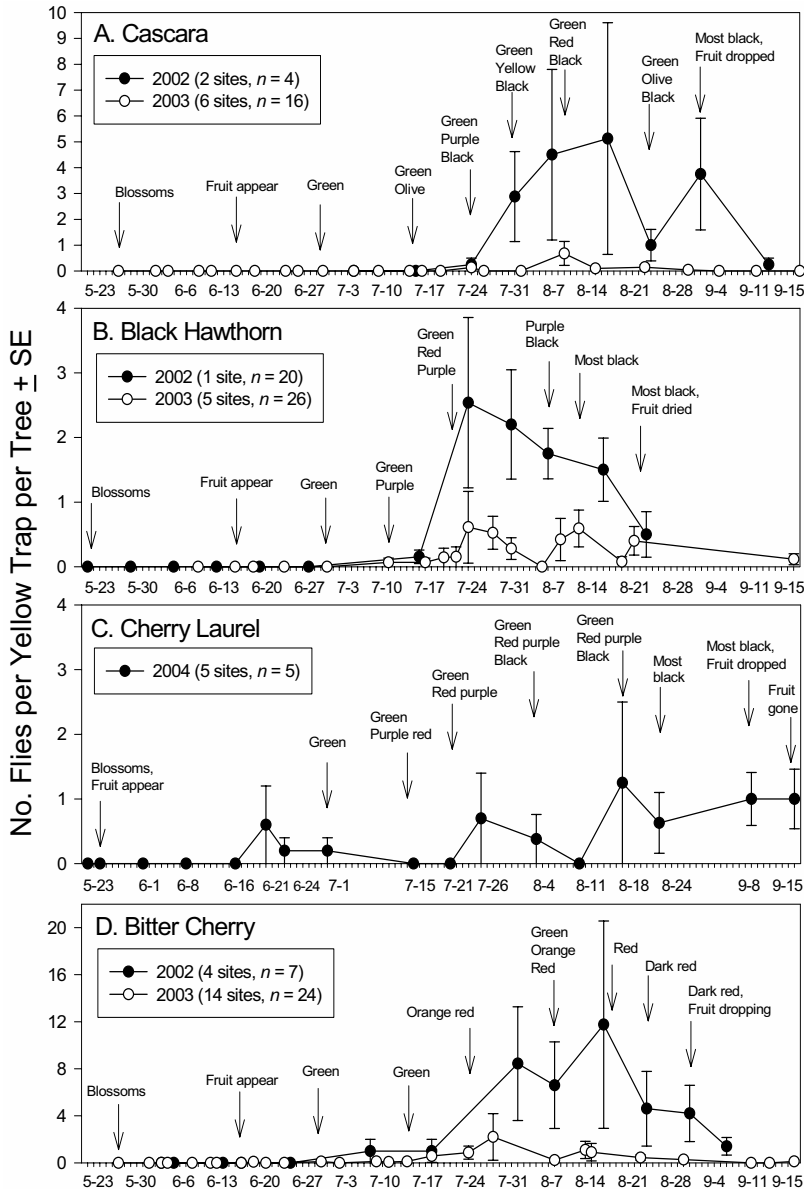


Fig. 2. Numbers of adult *R. indifferens* \pm SE caught on unbaited sticky yellow panel traps in four tree species, May to September in the coast forest ecosystem in the vicinity of Vancouver, WA. (A) Cascara, 2002 and 2003. (B) Black hawthorn, 2002 and 2003. (C) Cherry laurel, 2004. (D) Bitter cherry, 2002 and 2003. *n*, number of trees. Note different scales on y-axes. Elevations of sample sites were 3–305 m.

dental host. Cascara belongs to the Rhamnaceae (buckthorns) and is the first recorded developmental host of *R. indifferens* outside the Rosaceae. This suggests *R. indifferens* is not dependent on volatile and nutritional compounds unique to the rose family for host finding and larval development. Thus, *R. indifferens* does not strictly adhere to the definition of stenophagy (White et al. 2000). The variation in the wing pattern of one fly and the distinct wing pattern of another reared from cascara suggest that different phenotypes of *R. indifferens* from this host exist (see

below). Cascara had not been recorded as a host of any *Rhagoletis* (Smith and Bush 2000), or, to our knowledge, of any tephritid, although *Rhammus* was used by *R. pomonella* from apple as the main nonhost-feeding site in a study in Massachusetts (Hendrichs and Prokopy 1990).

Black hawthorn and cherry laurel were both suitable developmental hosts. Black hawthorn fruit yielded low numbers of *R. indifferens*, indicating infestation or larval development in this host is occasional. It is possible that, although the stinging re-

Table 3. Longevity (days), dry body mass (milligrams), and fecundity \pm SE of *R. indifferens* reared from pupae from different hosts collected in the field in Washington state, 2002 and 2003, under laboratory conditions

Host	Males				Females				
	<i>n</i>	Longevity	<i>n</i>	Dry mass ^a	<i>n</i>	Longevity	<i>n</i>	Dry mass ^a	No. eggs/fly ^b
Cascara	11	62.3 ± 11.7ab	9	0.571 ± 0.051a	8	55.5 ± 10.2ab	8	0.899 ± 0.065a	271.8 ± 120.3a
Black hawthorn	1 ^c	>26	1	0.622	2	79.5 ± 21.5	1	1.765 ± 0.114	
Cherry laurel	9 ^d	46.2 ± 7.8b	11	0.784 ± 0.063bc	18	37.7 ± 5.5a	16	1.011 ± 0.059a	
Bitter cherry	35	83.4 ± 5.2a	35	0.707 ± 0.023b	36	61.3 ± 5.1b	33	0.936 ± 0.049a	283.0 ± 47.9a
Sweet cherry	18	71.7 ± 8.8ab	16	0.807 ± 0.045c	17	59.5 ± 6.3b	11	1.340 ± 0.118b	368.8 ± 92.6a

Means followed by the same letter within columns are not significantly different (ANOVA, Fisher's LSD test, $P > 0.05$).

^a Not all flies used in longevity test were weighed because some were damaged and had missing body parts after the end of the test.

^b Data for 2002 flies only; four, 27, and 11 flies from cascara, bitter cherry, and sweet cherry, respectively.

^c Black hawthorn flies not included in statistical analysis; male sacrificed as a voucher specimen at 26 d.

^d Two that died at emergence not included.

sponse to hawthorn fruit was seemingly common, suggesting some degree of host acceptance based on chemical, visual, or tactile cues, stinging only occasionally led to oviposition. Another possibility is that hawthorn fruit is nutritionally poor for *R. indifferens* larvae and high mortality occurs in the fruit. Cherry laurel was heavily infested at some sites, suggesting it is commonly used by *R. indifferens*. The emergence of larvae from fruit collected in early September suggests that flies may use cherry laurel as an alternative resource after fruit on bitter cherry drop. Cherry laurel had not been recorded as a host of any *Rhagoletis* (Smith and Bush 2000), or, to our knowledge, of any tephritid.

The seasonal pattern of adult abundance was similar on cascara, black hawthorn, cherry laurel, and bitter cherry, which overlapped in their periods of fruit ripening. This suggests that, when one host fails to produce fruit in certain years, flies can disperse and use the fruit of the other hosts. Because of the different phenologies of the trees and the reported longevity of flies in the field (15–30 d in central Washington; Frick et al. 1954), most flies on the new hosts probably originated from bitter cherries and not from sweet and sour cherries. In the coast forest ecosystem, flies in sweet or sour cherry orchards emerge in May until mid July (AliNiazee 1976), when fruit are present on trees and before cascara, black hawthorn, cherry laurel, and bitter cherry fully ripen.

Adult flies used cascara and black hawthorn for activities other than oviposition. *R. indifferens* fed on the damaged fruit of these two hosts, the first records of *R. indifferens* feeding on a sugar source other than cherry in nature. Mating was commonly seen on cascara and black hawthorn, indicating flies had not merely mated on bitter cherry trees, dispersed, incidentally landed on the trees, and oviposited. Rather, it seemed feeding, mating, and oviposition all occurred on the new hosts. The use of black hawthorn also resulted in flies coupling with *R. pomonella*, the first report of *R. indifferens* engaged in such an interspecific interaction in nature. This behavior has been seen for *Rhagoletis fausta* (Osten Sacken) and *R. pomonella* on sour cherry (Prokopy and Bush 1973). *R. indifferens* and *R. pomonella* co-occurred on sour cherry in Utah (Messina and Subler 1995), but no sexual encounters between them were mentioned.

Flies reared from different hosts showed differences and similarities in several life history characteristics. Longevity of flies from cherry laurel was lower than that recorded from other hosts, but further examination is needed to determine whether this is biologically relevant or was an artifact of sample sizes. Low body mass of flies from cascara, cherry laurel, and bitter cherry was caused either by host fruit nutrition and size or were a genetically determined characteristic of flies infesting these hosts. The data suggest flies from cascara are as fecund as those from bitter cherries, although the sample size was low. This may indicate cascara provides adequate nutrition to larvae and produces reproductively normal adults or that adequate adult nutrition overrides any effect of deficient larval nutrition on egg production.

In the ponderosa pine and sagebrush–bunchgrass ecosystems, black hawthorn seemed not to be used by *R. indifferens* for adult activities (evidenced by the lack of flies on unbaited traps) and hence not for larval development. Several factors could affect the differential usage in ponderosa pine, sagebrush–bunchgrass, and coast forest ecosystems. In the ponderosa pine ecosystem, there were fewer hawthorns, the stands in general were scattered or isolated, and bitter cherries were present, perhaps keeping the flies mostly on the bitter cherries. In the sagebrush–bunchgrass ecosystem, the relatively few hawthorns, generally scattered trees, high July temperatures (Frick et al. 1954), and the lack of common native hosts probably reduce fly survival and keep flies mostly on the earlier developing sweet and sour cherries. Similarly, no native or alternate hosts were found in the warm, dry interior of British Columbia (Madsen 1970).

The possibility that host races (partially reproductively isolated populations specializing in different hosts (Diehl and Bush 1984)) of *R. indifferens* exist or that a new *Rhagoletis* species exists in the coast forest ecosystem in Washington should be explored. Host race formation has been well documented in *Rhagoletis* species (Bush 1969a, b), especially in *R. pomonella* (Feder et al. 1995, 1997a, b; McPherson et al. 1988). Based on the distinct wing patterns of two individuals and small body size, some flies attacking cascara could represent a new race or species, although more flies need to be examined and the biology of the flies

associated with this host needs to be studied thoroughly before any conclusions can be made.

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